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Environmental drivers of bloom-forming cyanobacteria in the Baltic Sea: Effects of salinity, temperature, and irradiance

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ABSTRACT

Environmental changes, including hydrological modifications caused by global warming, are one of the major drivers of harmful cyanobacterial bloom expansion. The ecophysiological study of bloom-forming filamentous cyanobacteria *Nodularia spumingena*, *Aphanizomenon* sp. and *Dolichospermum lemmermannii* was conducted in a series of laboratory tests. Cyanobacterial cultures were grown at various combinations of environmental conditions (scenarios). These scenarios were combinations of irradiance in the sense of Photosynthetically Active Radiation (PAR) spectrum (10, 100, 190 and 280 µmol photons $m^{-2}s^{-1}$), temperature (15, 20 and 25 °C) and salinity (3, 8 and 13). The cell concentration, pigment content and photosynthetic performance of cyanobacteria were measured to analyze the environmental stress. Generally, a positive effect of high irradiance and temperature on the abundance of these organisms as well as a preference to low salinity were observed. Pigment concentration (chlorophyll *a* (Chl *a*), carotenoids (Car) and Car/Chl *a* ratio), Chl *a* fluorescence and photosynthetic irradiance response (*P-E*) curves were used to characterize photoacclimation capacity of the cyanobacterial strains. The highest Car/Chl *a* ratio was observed at a high irradiance (190–280 µmol photons $m^{-2}s^{-1}$) and the lowest at 10 µmol photons $m^{-2}s^{-1}$ and 25 °C. Chl *a* fluorescence of cyanobacterial strains indicated that the highest irradiance (280 µmol photons $m^{-2}s^{-1}$) and the highest temperature (25 °C) had a negative effect on both the maximum quantum yield (F_v/F_m) and the effective quantum yield of photosystem II (PSII) photochemistry (ΦPSII). This effect was more pronounced in the case of ΦPSII than F_v/F_m. Based on photosynthesis irradiance response (*P-E*) curves, two mechanisms of photoacclimation were recognized. The maximum value of the photosynthetic capacity (P_m) expressed per unit biomass for cells grown at 10 µmol photons $m^{-2}s^{-1}$ indicated a change in the number of Photosynthetic Units (PSU). The constant values of the initial slope of the *P-E* curve (α) and the maximum value of P_m expressed per Chl *a* unit at 280 µmol photons $m^{-2}s^{-1}$ indicated another mechanism, a change in PSU size. The study showed a wide range of filamentous cyanobacteria responses to the changing environment. This may explain the successful growth of freshwater and brackish filamentous cyanobacteria in the Baltic Sea and suggests further expansion with progressing climate change.

1. Introduction

Cyanobacteria are one of the most ancient organisms on the planet with fossil remains dating back about 3.5 billion years (Paerl and Paul, 2012). Cyanobacteria harmful algal blooms (CyanoHABs) have been reported in the scientific literature for more than 140 years (Francis, 1878). However, in recent decades, the frequency and intensity of these blooms, as well as economic loss associated with these events has increased in aquatic ecosystems (O'Neil et al., 2012; Worden and Wilken, 2016; Paerl, 2018). Toxic blooms occurrence, distribution, and timing, are of crucial significance for the environmental and public health issues (Codd et al., 2005; Pearson et al., 2010; Leão et al., 2012; Mazur-Marzec et al., 2013; Testai et al., 2016).

Today, cyanobacteria enjoy a remarkably broad geographic distribution, ranging from polar to tropical regions in northern and southern hemispheres, where they are capable to dominate planktonic and benthic primary production in diverse habitats (Paerl and Paul, 2012; Paerl, 2018). Filamentous and potentially toxic cyanobacteria were identified even in the bioaerosols of the coastal area posing a serious threat to human health in the Baltic Sea region (Lewandowska

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et al., 2017). In order to predict the massive occurrence of cyanobacteria blooms the identification of the causes and understanding the interactions that underlie the observed correlations is of primary concern (Worden and Wilken, 2016). Prevention and reduction of the negative impact of the blooms will be the biggest challenge of the next years (O'Neil et al., 2012; Funkey et al., 2014; Brutemark et al., 2015; Worden and Wilken, 2016; Paerl, 2018).

In this study three species of filamentous cyanobacteria were examined: *Nodularia spumigena*, *Aphanizomenon* sp., and *Dolichospermum lemmermannii*. These species are known as heterocystous nitrogen-fixing and bloom forming species of the Baltic Sea (Stal et al., 2003; Wasmund, 2017), of which *Dolichospermum lemmermannii* and *N. spumigena* can produce toxins and other harmful secondary metabolites (Stal et al., 2003; Mazur-Marzec et al., 2015; Teikari, 2018). Whether the Baltic *Aphanizomenon* sp. can produce toxins is still an open question (Janson et al., 1994). Generally, this species is not assumed as toxic in the Baltic Sea (Laamanen et al., 2002, Repka et al., 2004). However, note that not only toxins are a negative effect of large blooms on the ecosystem. For another harm stands, for instance, dead zones areas extension. After massive blooms, the plankton die and fall to the seafloor, where they are digested by microorganisms. This process reduces the oxygen level at that locality and results in development of low-oxygen zones, called dead zones. The interannual extension of dead zones area is strongly pronounced in the Baltic (Feistel et al., 2016). Since *N. spumigena*, *Dolichospermum lemmerani* and *Aphanizomenon* sp. form large blooms, they may be assumed as a contributor in the dead zones continuous expansion in the Baltic Sea.

Many different factors, including physical parameters, availability, and competition for resources, selective grazing and allelopathic interactions may affect the occurrence of harmful blooms in aquatic ecosystems (Whitton and Potts, 2012; Barreiro Felpeto et al., 2018a; Paerl, 2018). As shown by recent research, increase in the frequency and duration of toxic cyanobacterial blooms, especially in lakes, might be directly and indirectly related to anthropogenic activities (Scholz et al., 2017). Specifically, the input of inorganic nutrients to waters tends to support the phytoplankton growth in general and a range of HAB species in particular (Davidson et al., 2014). On the one hand, cyanobacterial blooms are possible only when multiple favorable factors act simultaneously rather than due to a single environmental driver (Heisler et al., 2008). On the other, it has been suggested that global climate change and higher water surface temperature could be the main reason of the further increase in cyanobacterial blooms (El-Shehawy et al., 2012; Paerl and Paul, 2012).

Cyanobacterial blooms have become more pronounced and frequent since the 1960s than in the late 19th and early 20th centuries (Finni et al., 2001). This is likely because of a combination of human-induced eutrophication and climate change (Nutman et al., 2016). Eutrophication is an increase in the nutrient concentration in the basin, which results in the basin's trophy increase. For the Baltic Sea, eutrophication is claimed to be a serious threat (HELCOM, 2014, 2018). The nutrient level has a significant impact on the Baltic bloom initiation and development (e.g., Stal et al., 1999; Teikari, 2018). In the Bothnian Bay, filamentous cyanobacteria blooms do not appear because of the phosphorus deficiency, phosphorus being depleted in the Bothnian areas (elevated N:P ratio) (Alasaarela, 1979; Karjalainen et al., 2007; Andersson et al., 2015a). On the contrary to that, nitrogen depletion leads to lower N:P ratios and favors diazotrophic taxa e.g., *N. spumigena*, *Aphanizomenon* sp. and *Dolichospermum* sp. Changes applied to the half-saturation rate for nutrients in the ecological numerical models (adjustment during model calibration) reveal a strong impact on the overall model results (Neumann et al., 2002). This implies that not only the concentration of nutrients but also the specific preferences of the organisms influence their growth and competition with others. On the other hand, some studies pointed out to an increasing trend in the algal biomass in the Baltic Sea region in 1952–1992, which was related to the decreasing trend of radiation (Russak, 1994). The fact that light is a limiting factor for phytoplankton bloom in the Baltic Sea cannot be ignored. The study implied that eutrophication may even have overcompensated for the reduction in light. An aspect indirectly related to the light conditions is the fact that filamentous cyanobacteria are planktonic. Phytoplankton cells are dragged by water masses up and down. This vertical movement influences the time of cell exposure to the full sunlight (at the sea surface). Furthermore, the amount of available solar radiation decreases with depth at a different pace depending on the inherent optical properties of the water (Mobley, 2004). The vertical location in the water column is determined mainly by currents, wind-driven vertical mixing, and water stratification. For instance, warming of the water surface leads to a more stable stratification of the water column, resulting in less vertical mixing (Elliott, 2010; Paerl and Huisman, 2009). According to Wasmund (1997), filamentous cyanobacteria of *N. spumigena* and *Aphanizomenon* sp. prefer weak wind conditions resulting in the well-stratified water column. Wasmund (1997) reported a bloom to break when the weather conditions are poor with low irradiation or high wind speed. Diurnal vertical migrations of cyanobacteria allows them to take advantage of both light at the surface and nutrients in deeper waters (Villareal and Carpenter, 2003). Despite that, the move itself may, however, have an additional negative impact on the filamentous cyanobacteria structure, which is a mechanical damage of filaments. Moreover, Visser et al. (2016) showed vertical mixing (artificially generated in the lake for the purpose of that study) to bring about a change in phytoplankton dominance structure from cyanobacterial dominance to that of green algae and diatoms. This was observed when the imposed mixing was strong enough to keep the cyanobacteria entrained in the turbulent flow, and the mixing was deep enough to limit light availability.

Cyanobacteria have developed numerous adaptive strategies which enable them to survive in extreme conditions. They are able to thrive under high insolation and produce a significant amount of biomass in the Baltic Sea that forms massive blooms visible by the Earth observation satellites (S1 Fig; symbol 'S' before the Figure or Table number indicates the supplementary material).

Recent investigations confirmed that filamentous cyanobacteria are a dominant phytoplankton group during summer blooms in the Baltic Sea. Wacklin et al. (2009) reported *N. spumigena*, *Aphanizomenon* sp. and *Dolichospermum* sp. to be the most abundant cyanobacteria in the Baltic Sea Proper (BSP) in the summer season. Moreover, Bianchi et al. (2000) defined them as an important natural component of the pelagic ecosystem in the area since these organisms fix 180–430 $\times$ 10^9 g N each year, an amount similar to the total annual riverine nitrogen input to the BSP (Gulf of Finland excluded) (Larsson et al., 2001). Furthermore, they can contribute a third of the total Chl *a* concentration (a proxy for phytoplankton biomass) (Stal et al., 1999; Stal and Walsby, 2000).

The functioning of *N. spumigena*, *Aphanizomenon* sp. and *Dolichospermum* sp. differs between species. *Aphanizomenon* sp. vegetative filaments are present in the Baltic waters within the course of a whole year and according to Laamanen (1996) they were found underneath the ice cover in the Bothnian Bay. Generally, these vegetative filaments surviving the winter in the water body may be sufficient for the perennation of *Aphanizomenon* sp. (Jones, 1979) since no akinete formation was observed in the southern Baltic Sea (Palińska and Surosz, 2008). Contrary to that, the akinete formation plays a key role in the annual survival of the Baltic *Dolichospermum* sp. (Hellweger et al., 2008; Suikkanen et al., 2010). Regarding *Nodularia spumigena*, it is not registered in the surface water after the bloom (transitory species) (Wasmund, 2017). The life cycle of that species can be divided into three phases: germination, potential growth in the sediment, and migration to the pelagial (Kononen, 1992; Karlsson-Elfgren and Brunberg, 2004; Hense and Beckmann, 2006). *N. spumigena* filaments are scarce in the winter sampling (Wasmund, 1997) on the one hand but on the other, this species is able to overwinter in the ice (Laamanen, 1996). There has been the akinete formation of *N. spumigena* observed in the Baltic Sea however these observations were very rare (Albertano et al.,

1996). Thus, the complete life cycle of the *Nodularia spumigena* and the population the blooms are originated in are still not sufficiently known (Wasmund, 2017).

Both archive measurements and satellite data confirm that the biomass of harmful and bloom-forming cyanobacteria seem to have increased due to global warming (Finni et al., 2001; Kahru and Elmgren, 2014). Additionally, according to a long-term predictive numerical study conducted for the Baltic Sea area, the season favored by cyanobacteria to bloom may be prolonged in the future (Neumann, 2010). Since some of the cyanobacteria are heterocystous and diazotrophic, they play a pivotal role in the nutrient cycle in the aquatic environments, particularly with respect to eutrophication and at the climate change (Paerl and Paul, 2012). Many field studies have been conducted to determine responses of cyanobacterial blooms in aquatic ecosystems all over the world (Stramska and Dickey, 1993; Pliński et al., 2007; Davidson et al., 2014). However, it is still poorly understood why the timing and magnitude of their blooms differ remarkably from one year to the next at the same location (Cebrian and Valiela, 1999). This is also the case in the Baltic Sea (Hagen and Feistel, 2008). For this reason, it is important to analyze the cyanobacteria physiology as a response to changing environmental conditions.

The overall goal of this study was to describe the physiological response of bloom-forming diazotrophic cyanobacteria *N. spumigena*, *Aphanizomenon* sp. and *D. lemmermannii* (=*Anabaena lemmermannii*) to different environmental conditions as elucidated by laboratory tests. According to authors' best knowledge, such a detailed analysis, for such a wide range of conditions, equivalent to those in the natural environment has not been conducted for these organisms yet. Physiological responses of cyanobacteria to a series of combinations of salinity, temperature and Photosynthetically Active Radiation (PAR) were analyzed. The physiological response here is observed based on the change in cell concentration, pigment content, Chl *a* fluorescence characteristics and photosynthesis parameters. In addition, photoacclimation mechanisms were analyzed.

2. Material and methods

2.1. Material and tests conditions

The tests were conducted on the filamentous cyanobacteria: *Nodularia spumigena* (BA-15), *Aphanizomenon* sp. (BA-69) and *Dolichospermum lemmermannii* (KAC-16). The strains were isolated from the Baltic Sea and maintained as unialgal cultures in the Culture Collection of Baltic Algae (CCBA) at University of Gdańsk, Poland and Kalmar Algae Collection (KAC) at Kalmar University, Sweden. In KAC, *Dolichospermum lemmermannii* is still recorded as *Anabaena lemmermannii*.

The tests on the 'batch cultures' were carried out in 25-mL glass Erlenmeyer flasks containing sterilized f/2 medium (Guillard, 1975) with a sufficient nutrient level (the medium contains sufficient amount of mineral salts to support algal culture without further enrichment). The cultures were not limited by nutrients. The impact of nutrient level changes on the cyanobacteria growth was not examined in this study. The media were prepared from distilled water, previously filtered through glass fiber filters (Whatman GF/C, Pittsburgh, USA) and autoclaved. The flasks with cyanobacteria were swirled daily during the experiments. The cyanobacteria were incubated under a 16:8 h light:dark cycle at four irradiance levels (10, 100, 190 and 280 μmol photons $m^{-2}s^{-1}$), three temperatures (15, 20 and 25 °C) and three salinities (3, 8 and 13). The intensity of PAR was measured using a quantum-meter (LI-189, LI-COR Inc., Nebraska, USA) with a scalar collector. The tests were conducted in incubators capable of maintaining constant temperature (± 1 °C). Media differing in salinity were obtained by dissolving an appropriate amount of Tropic Marine Synthetic Sea Salt in a specific volume of distilled water. The salinity of the medium was measured by a salinometer (inoLabCond Level 1, Weilheim in Oberbayern, Germany). The light intensity of 10–280 photons $m^{-2}s^{-1}$ is equivalent to the sunlight levels of 2–62 $W m^{-2}$ (Sager and McFarlane, 1997). These are relatively low, but realistic light levels in comparison to the average values observed in the Baltic Sea (reported by Leppäranta and Myrberg, 2009) or modelled from data derived in 2017 (www.satbaltyk.pl). The average surface water salinity (above the halocline) in the Baltic Sea varies between 2 and 4 in the Bay of Bothnia to 18–26 in Kattegat (Leppäranta and Myrberg, 2009). This points to the strong horizontal salinity gradient in the Baltic area. The multi-year mean temperatures in surface waters are assumed to be up to 18 °C (Leppäranta and Myrberg, 2009). However, recent publications claim that this value has risen up to 20 °C (Snoeijs-Leijonmalm and Andrén, 2017). Siegel and Gerth (2017) reported the Sea Surface Temperature (SST) to be higher than 20 °C in the whole Baltic Sea area excluding the Danish Straits, Bothnian Bay, and northern Bothnian Basin in the warmest week of 2016, in July. Furthermore, according to modelled data, SST in the Baltic Sea was higher than 25 °C in summer 2018 (www.satbaltyk.pl). Overall, the environmental conditions set in the tests are representative of the area of study. These settings made the present results comparable to data obtained in the autecology study of Baltic picocyanobacteria in the recent paper by the authors (Śliwińska-Wilczewska et al., 2018) and in other studies on filamentous cyanobacteria reported in the literature (e.g., Jodłowska and Latała, 2010; Jodłowska and Śliwińska, 2014). In those studies, the synthetic environmental conditions were intentionally set at similar levels. Furthermore, the aim was also to compare the ecophysiology of Baltic filamentous cyanobacteria to ecophysiology of the Baltic picocyanobacteria analyzed by Śliwińska-Wilczewska et al. (2018). The cyanobacterial cultures were acclimated to environmental conditions for 2 days. Afterward, the actively growing cultures served as an inoculum for test cultures where the initial number of cells was 10^6 cells mL^{-1}. The test cultures were grown in 3 replicates and were incubated for one week at each combination of light, temperature, and salinity. There was 20 mL of the actual culture in each flask. On the last day of the experiment, 6 mL of cyanobacterial cultures were collected from each replica for analysis; 2 mL for cell density, 2 mL for chlorophyll fluorescence, and 2 mL for photosynthesis rate investigations. The rest of the cultures volumes from each replica were used for the photosynthetic pigments analysis.

2.2. Calculation of cell density

Cell density in the monocultures was estimated with previously determined linear regression models relating the cell concentration (N mL^{-1}) to optical density (OD) (Śliwińska-Wilczewska et al., 2017; Barreiro Felpeto et al., 2018b). Cyanobacteria cells were counted under a light microscope (Nikon Eclipse 80i, Nikon, Tokyo, Japan) in the Bürker counting chamber (48 squares per count) following the procedure described by Guillard and Sieracki (2005). The cell abundances of *N. spumigena*, *Aphanizomenon* sp. and *D. lemmermannii* were estimated from filament size data. One filament unit was regarded as equal to 100 μm of a filament. The filament units were counted and the units were converted to cell numbers (1 filament unit = 20, 10, 10 cells for *N. spumigena*, *Aphanizomenon* sp. and *D. lemmermannii*, respectively). OD was measured spectrophotometrically at 750 nm with a Multiskan GO UV-VIS spectrophotometer (Thermo Scientific, Massachusetts, USA). The data were used to fit a linear regression model between the variables: cell concentration and OD. For *N. spumigena*, *Aphanizomenon* sp. and *D. lemmermannii*, the correlation coefficients of their respective linear regression models were $r = 0.98$, $r = 0.99$ and $r = 0.97$, and the model equations were: y [N mL^{-1}] = $20{\cdot}12.4{\cdot}10^5$x-$6.0{\cdot}10^3$, y [N mL^{-1}] = $10{\cdot}30.0{\cdot}10^6$x-$9.5{\cdot}10^4$ and y [N mL^{-1}] = $10{\cdot}25.7{\cdot}10^6$x-$8.6{\cdot}10^4$, respectively, where y = cell concentration and x = OD. Cell concentrations were calculated on day 7 of the laboratory tests.

2.3. Measurement of pigment contents

Chl *a* and Car concentrations in the analyzed cyanobacteria were measured spectrophotometrically according to Strickland and Parsons (1972). Chl *a* and Car were extracted with cold 90% acetone in the dark for 24 h at −60 °C. To remove cell debris and filter out particles, the extracts were centrifuged at 13,000 rpm for 2 min (Sigma 2–16P, Osterode am Harz, Germany). The extinction values were determined at 480, 664 and 750 nm in a DU530 UV-VIS Life Science spectrophotometer (Beckman, California, USA) equipped with a 1 cm glass cuvette.

2.4. Chlorophyll fluorescence analysis

Chlorophyll *a* fluorescence was measured with a Pulse Amplitude Modulation (PAM) fluorometer (FMS1, Hansatech, King's Lynn, Norfolk, UK), using a 594 nm amber modulating beam with a 4-step frequency control as the measuring light. Samples for chlorophyll *a* fluorescence analysis were collected after 7 days of the tests. The samples were filtered through 13-mm glass fiber filters (Whatman GF/C, pore size = 1.2 μm). Before the measurement, the filtered sample was kept in the dark for approximately 10 min. The maximum PSII quantum efficiency (F_v/F_m) and effective quantum yield of PSII photochemistry (ΦPSII) were calculated (Campbell et al., 1998).

Chlorophyll *a* fluorometry is a common, non-invasive method of assessing physiological status and photosynthetic performance in micro-algal mass cultures. Fluorescence and (relative) electron transport rate can be correlated with the overall photosynthetic performance and obtain rough estimates of productivity (Malapascua et al., 2014). However, recent studies revealed that the fluorescence F_0 is related to light absorption capacities rather than to the chlorophyll concentration. The light availability, nutrient status or temperature have significant impact on the photosynthetic apparatus, especially *PSII* that influences the measurement of Chl *a* fluorescence yield. The micro-algal species might show endogenous diurnal patterns in fluorescence due to the cellular metabolism changes (Malapascua et al., 2014; Matorin et al., 2004). The ratio between the chlorophyll *a* and the total photosynthetic pigment content in algal cells may be estimated only after careful calibration of F_0 with respect to Chl *a*, and spectrophotometry is recommended.

2.5. Measurement of photosynthesis rate

Oxygen evolution was measured on day 7 of the test with a Clark-type oxygen electrode (Chlorolab 2, Hansatech). The temperature was controlled with a cooling system LAUDA (E100, Germany). Irradiance was measured with a quantum sensor (Quantitherm, Hansatech, King's Lynn, Norfolk, UK). Test data were fitted to the photosynthesis irradiance response (*P-E*) curves using the equation developed by Jassby and Platt (1976) and Statistica® 13.1 software, and the relevant photosynthesis parameters, i.e., the photosynthetic capacity (P_m) and the initial slope of the *P-E* curve (α) were estimated (Sakshaug et al., 1997). Changes in Photosynthetic Unit (PSU) number and sizes reflecting the photoacclimation mechanism were examined (Richardson et al., 1983).

2.6. Statistical analyses

Effects of the factors investigated and their interaction on the cell concentration, pigment content, fluorescence parameters and photosynthetic performance of *N. spumigena*, *Aphanizomenon* sp. and *D. lemmermannii* were explored with factorial tests. Two-way analysis of variance (ANOVA) was used to assess the main effects of individual factors and the main effects of factor interaction on the parameters studied. The independent variables were temperature and irradiation in each salinity medium, whilst the dependent variable was always the measured parameter, e.g., cell concentration. In order to analyze the potential Type II error, the power tests were performed for this study. The software Gpower 3.1.9.2 (Faul et al., 2007) was used for it. The power test was performed with the large effect size applied (0.4) and pointed to the sufficient sample size to be given significant statistical results (Cohen, 1969, p. 348; Faul et al., 2009) since in this study the data sample is 12 discrete results, in 3 replicas (36) applied in 3 different mediums of salinity. The Type II error for F tests ANOVA has been calculated for the statistical significance level (α) of 90% and 95% and equaled 35% (the power of the test 65%) and 49% (the power of the test 51%), respectively. A post hoc test (Tukey's HSD) was used to test for differences between treatment levels. Levels of statistical significance were: $^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$. Data are reported as the means ± standard deviations (SD). In the factorial test, values of independent variables occurred at the same intervals. All the tests were run in triplicate. This made it possible to develop mutually orthogonal polynomials. Polynomial fitting with ξ′ was simplified by the use of orthogonal polynomial tables (Fisher and Yates, 1963). The method allowed to determine the influence of each environmental factor separately and of factor interaction on the parameters measured. To this end, regression equations describing relationships of the factors and the parameters examined were developed. The statistical analyses were performed using Statistica® 13.1 software and the figures were prepared using the R software version 0.3–41 (https://cran.r-project.org/web/packages/scatterplot3d/).

3. Results

3.1. Cyanobacterial culture concentration

In general, factorial tests showed that both irradiance and temperature had a promoting effect on the cyanobacterial culture concentration in each salinity tested (Fig. 1). Both light and temperature significantly affected the cell concentration of *N. spumigena* (ANOVA, $F_{6,24} = 1088.0$, $p < 0.001$, ANOVA, $F_{6,24} = 1425.1$, $p < 0.001$ and ANOVA, $F_{6,24} = 1546.7$, $p < 0.001$, for 3, 8, 13, respectively), *Aphanizomenon* sp. (ANOVA, $F_{6,24} = 1165.2$, $p < 0.001$, ANOVA, $F_{6,24} = 815.4$, $p < 0.001$ and ANOVA, $F_{6,24} = 410.2$, $p < 0.001$, for 3, 8, 13, respectively) and *D. lemmermannii* (ANOVA, $F_{6,24} = 3481.7$, $p < 0.001$, ANOVA, $F_{6,24} = 1824.7$, $p < 0.001$ and ANOVA, $F_{6,24} = 1420.8$, $p < 0.001$, for 3, 8, 13, respectively). Moreover, ANOVA results indicated that in each cyanobacteria species the effect of temperature on the culture concentration was higher than the influence of irradiance and the interaction of the two factors (S1 Table). The maximum cell concentration (about 12×10^6 cell mL^{-1}) was noted for *Aphanizomenon* sp., at 100 μmol photons $m^{-2}s^{-1}$ light intensity, 25 °C and salinity 8 (Fig. 1B), and it was about 4.8 times higher than the minimum. The minimums were obtained at 10 μmol photons $m^{-2}s^{-1}$, 15 °C and salinity 13 (2.5×10^6 cell mL^{-1}). For *N. spumigena* (Fig. 1A) and *D. lemmermannii* (Fig. 1C) the maximum cell concentrations (3.4×10^6 cell mL^{-1} and 3.9×10^6 cell mL^{-1}, respectively) were recorded at the highest light intensity (280 μmol photons $m^{-2}s^{-1}$) and the highest temperature (25 °C). On the other hand, the minimum values were obtained at 10 μmol photons $m^{-2}s^{-1}$ and 15 °C (1.3×10^6 cell mL^{-1} and 0.9×10^6 cell mL^{-1}, respectively). Moreover, the maximum cell concentration for *N. spumigena* was found at salinity 13, whereas the maximum cell concentration of *D. lemmermannii* was detected at salinity 3.

3.2. Pigment content

In all the strains, the cell-specific (pg $cell^{-1}$) and mL-specific (μg mL^{-1}) pigment contents were environmentally driven (S2-S5 Figs). In general, in the three species, the cell-specific and mL-specific concentrations of Chl *a* and Car were negatively affected by high irradiance in the whole range of temperature and salinity. The highest Chl *a* and Car contents were measured in *N. spumigena* (0.907 and 0.234 pg

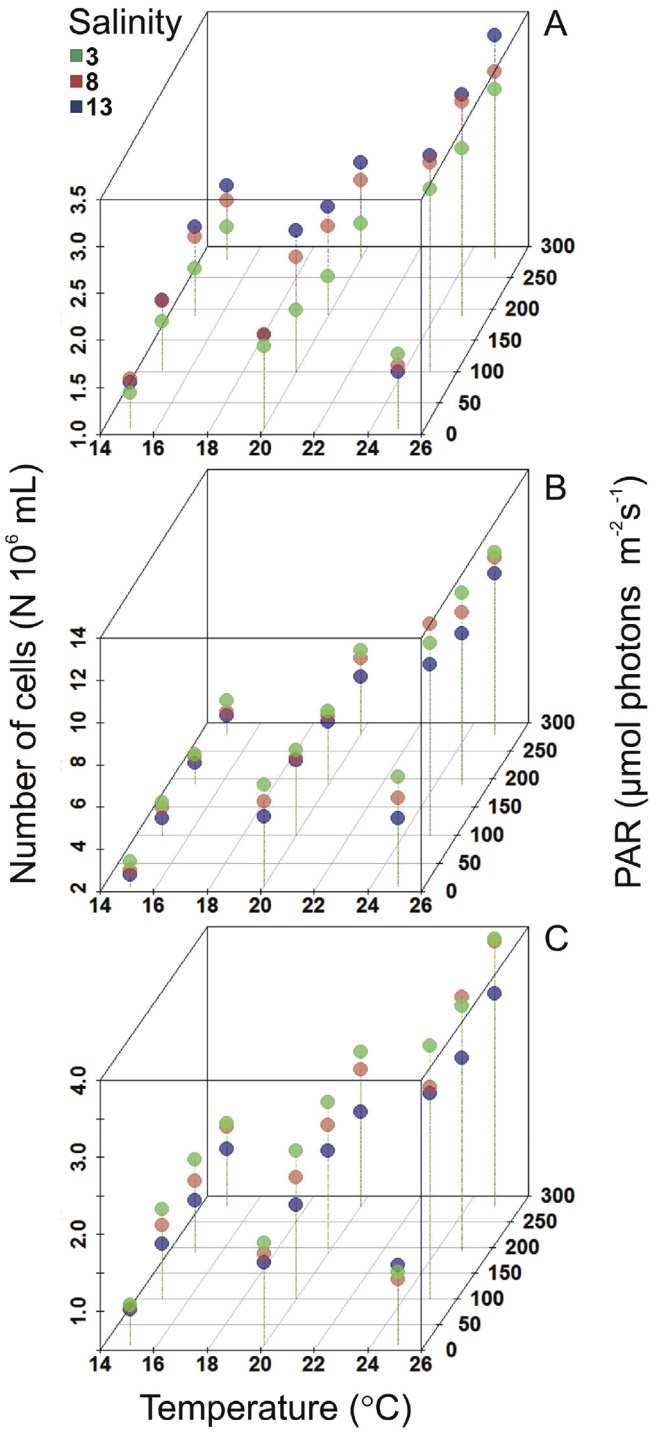

Fig. 1. Cell concentrations (10^6 cell mL^{-1}) of cyanobacterial strains: *N. spumigena* (A), *Aphanizomenon* sp. (B) and *D. lemmermannii* (C) after 7 d of cultivation at different PAR, temperature and salinity.

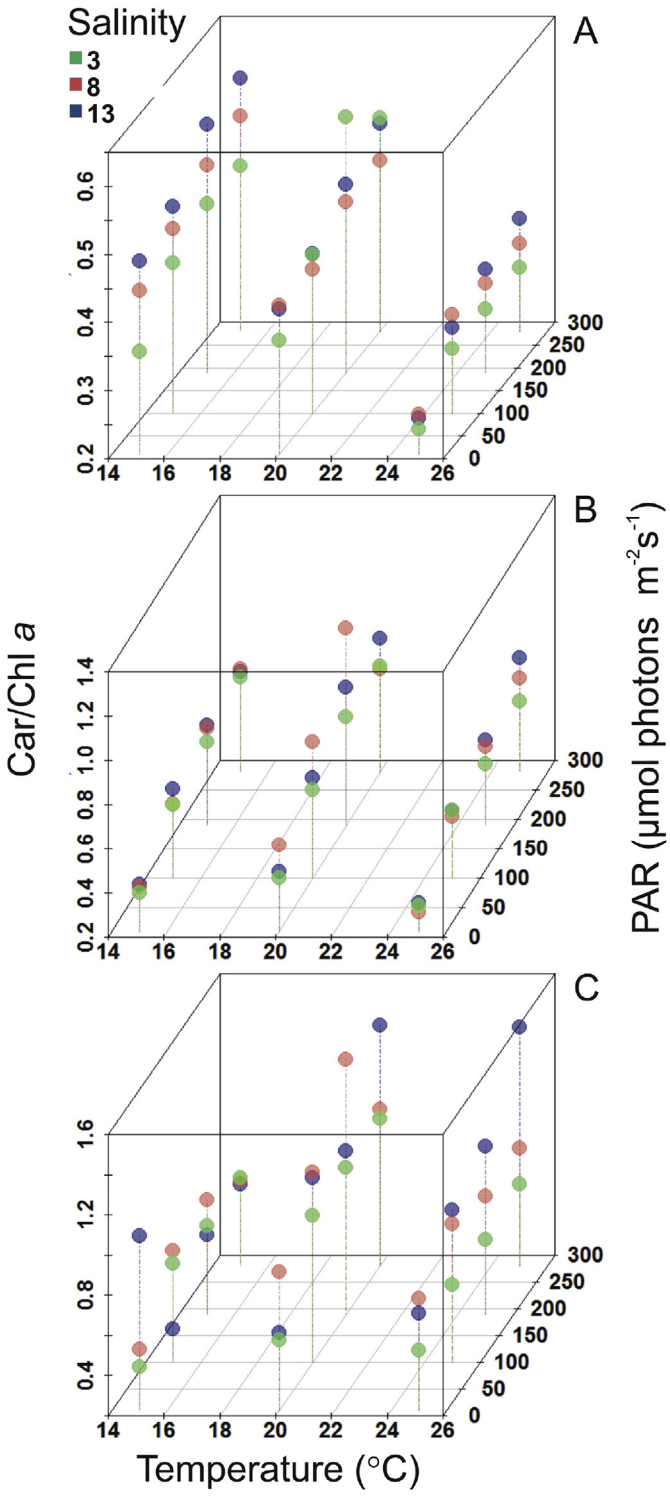

Fig. 2. Car/Chl *a* ratios in cyanobacterial strains: *N. spumigena* (A), *Aphanizomenon* sp. (B) and *D. lemmermannii* (C) after 7 d of cultivation at different PAR, temperature and salinity.

cell^{-1}, respectively) at 10 µmol photons $m^{-2}s^{-1}$, 25 °C and salinity 8 (S3A, b and S5A, b Figs), the lowest contents being found in *D. lemmermannii* (0.035 and 0.041 pg cell^{-1}, respectively) at 190–280 µmol photons $m^{-2}s^{-1}$, 20 °C and salinity 13 (S3C, c and S5C, c Figs).

Irradiance and temperature as well as their interaction significantly affected the Car/Chl *a* ratio in *N. spumigena* (ANOVA, $F_{6,24} = 2.8$, $p < 0.05$, ANOVA, $F_{6,24} = 5.4$, $p < 0.01$ and ANOVA, $F_{6,24} = 8.8$, $p < 0.001$, for 3, 8, 13, respectively), *Aphanizomenon* sp. (ANOVA, $F_{6,24} = 13.4$, $p < 0.001$, ANOVA, $F_{6,24} = 2.8$, $p < 0.05$ and ANOVA, $F_{6,24} = 6.2$, $p < 0.001$, for 3, 8, 13, respectively) and *D. lemmermannii* (ANOVA, $F_{6,24} = 6.8$, $p < 0.001$, ANOVA, $F_{6,24} = 1.8$, NS, $p > 0.05$ and ANOVA, $F_{6,24} = 4.9$, $p < 0.01$, for 3, 8, 13, respectively). ANOVA indicated that in *N. spumigena* and *D. lemmermannii,* the effect of temperature on Car/Chl *a* ratio was higher than the effect of irradiance and the interaction of both factors. In contrast, the Car/Chl a ratio of *Aphanizomenon* sp. at the lowest and the highest salinity, was more affected by irradiance than by temperature and by the interaction of both factors (S2 Table). The lowest values of Car/Chl *a* ratio in *N.*

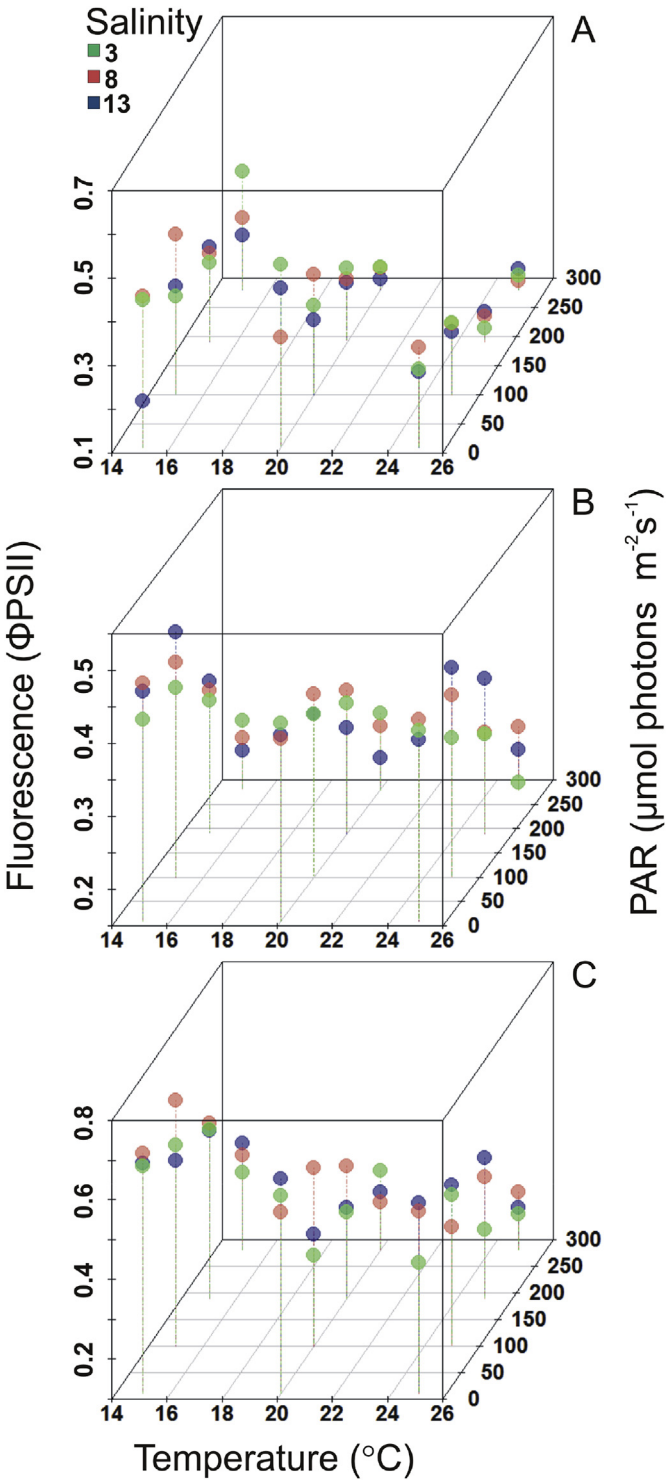

Fig. 3. The effective quantum yield of PSII photochemistry (ΦPSII) for cyanobacterial strains: *N. spumigena* (A), *Aphanizomenon* sp. (B) and *D. lemmermannii* (C) after 7 d of cultivation at different PAR, temperature and salinity.

spumigena and *Aphanizomenon* sp. were noted at 10 µmol photons $m^{-2}s^{-1}$, 25 °C and salinity 3 (0.236 and 0.314, respectively) (Fig. 2A and Fig. 2B). These minimums were 41% (for *N. spumigena;* equal to 0.572) and 29% (for *Aphanizomenon*; equal to 1.090) of the maximums for respective species. The maximums were obtained at PAR of 190–280 µmol photons $m^{-2}s^{-1}$, 15–20 °C and salinities 8–13. On the other hand, the highest values of pigment ratio in *D. lemmermannii*, recorded at 190 µmol photons $m^{-2}s^{-1}$, 20 °C and salinity 8 (1.463, Fig. 2C) was 4.03 times higher than the lowest values observed at the light intensity of 100 µmol photons $m^{-2}s^{-1}$, 15 °C and salinity 13 (0.363).

3.3. Chl a fluorescence parameters

Fluorescence measurements of the cyanobacterial strains showed the highest irradiance (280 µmol photons $m^{-2}s^{-1}$) and the highest temperature (25 °C) to have a negative effect on F_v/F_m (S6 Fig.) and ΦPSII (Fig. 3), the effect being pronounced in ΦPSII. Light and temperature were found to significantly affect ΦPSII of *N. spumigena* (ANOVA, $F_{6,24} = 31.8$, $p < 0.001$, ANOVA, $F_{6,24} = 18.8$, $p < 0.001$ and ANOVA, $F_{6,24} = 422.6$, $p < 0.001$, for 3, 8, 13, respectively), *Aphanizomenon* sp. (ANOVA, $F_{6,24} = 7.2$, $p < 0.001$, ANOVA, $F_{6,24} = 25.5$, $p < 0.001$ and ANOVA, $F_{6,24} = 17.8$, $p < 0.001$, for 3, 8, 13, respectively) and *D. lemmermannii* (ANOVA, $F_{6,24} = 29.5$, $p < 0.001$, ANOVA, $F_{6,24} = 10.4$, $p < 0.001$ and ANOVA, $F_{6,24} = 5.4$, $p < 0.01$, for 3, 8, 13, respectively). Furthermore, ANOVA indicated that the effect of irradiance on ΦPSII in all the cyanobacteria was higher than the influence of temperature and the interaction of both factors. The only exception was *N. spumigena*, in which ANOVA showed the influence of temperature on ΦPSII to be slightly higher than the influence of irradiance and the interaction of both factors, at the lowest salinity (S3 Table). The highest ΦPSII in *N. spumigena* (0.518) was observed in the lowest light intensity scenario (10 µmol photons $m^{-2}s^{-1}$), 20 °C and salinity 3 (Fig. 3A). On the other hand, the lowest ΦPSII (0.120) was observed at the highest light of 280 µmol photons $m^{-2}s^{-1}$, 25 °C and salinity 8. Conversely, for *Aphanizomenon* sp. (Fig. 3B) and *Dolichospermum* sp. (Fig. 3C) the highest values of ΦPSII were found at 100 µmol photons $m^{-2}s^{-1}$, 15 °C and salinity 8–13 (*Aphanizomenon* sp.: 0.486 and *Dolichospermum* sp.: 0.716) and were 2.37 and 3.46 times higher, respectively, than the minimums obtained at PAR 280 µmol photons $m^{-2}s^{-1}$, 20–25 °C and salinity 13 (*Aphanizomenon* sp.: 0.205 and *Dolichospermum* sp.: 0.207).

3.4. Photosynthesis

In all the cultures, the photosynthesis parameters: photosynthetic capacity and the initial slope of the *P-E* curve (P_m and α, respectively) were estimated for Chl *a*-specific and cell-specific domains (Figs. 4 and 5). The factorial tests and ANOVA allowed to determine effects of the factors investigated and their interaction on the photosynthesis parameters. The results are summarized in S4-S7 Tables.

Generally, the cell-specific P_m (µmol O_2 [cell 10^9]$^{-1}h^{-1}$) values were the highest in *N. spumigena* and *Aphanizomenon* sp. strains grown under the lowest light intensity. Conversely, the highest cell-specific P_m values in *D. lemmermannii* were observed at the highest light intensity. The maximum values of P_m in *N. spumigena*, *Aphanizomenon* sp. and *D. lemmermannii* were about 915.5, 451.3 and 586.7, respectively. When the parameters were related to Chl *a* unit, the values of P_m (µmol O_2 [µ Chl *a*]$^{-1}h^{-1}$) were similar to those expressed per cell unit. The maximum values of Chl *a*-specific P_m for *N. spumigena*, *Aphanizomenon* sp. and *D. lemmermannii* were 2.1, 1.6 and 8.1, respectively (Fig. 4). Moreover, the differences in Chl *a*-specific P_m in *Aphanizomenon* sp. and *D. lemmermannii* caused by irradiance were not statistically significant at salinity 8 (S5 Table).

The cell-specific α was dependent on the light intensity and temperature as well as on salinity (S6 Table). The maximum values of the cell-specific α (µmol O_2 [cell 10^9]$^{-1}h^{-1}$ [µmol photons $m^{-2}s^{-1}$]$^{-1}$) in *N. spumigena* and *Aphanizomenon* sp. (10.691 and 4.569, respectively) occurred in the scenario with 10 µmol photons $m^{-2}s^{-1}$, 15 °C and salinity 8–13. On the other hand, the maximum value of the cell-specific α in *D. lemmermannii* (5.632) was obtained at 280 µmol photons $m^{-2}s^{-1}$, 25 °C and salinity 3. When the rate of photosynthesis was related to Chl *a* unit, the values of α (µmol O_2 [µ Chl *a*]$^{-1}h^{-1}$ [µmol photons $m^{-2}s^{-1}$]$^{-1}$) in *D. lemmermannii* were different than those

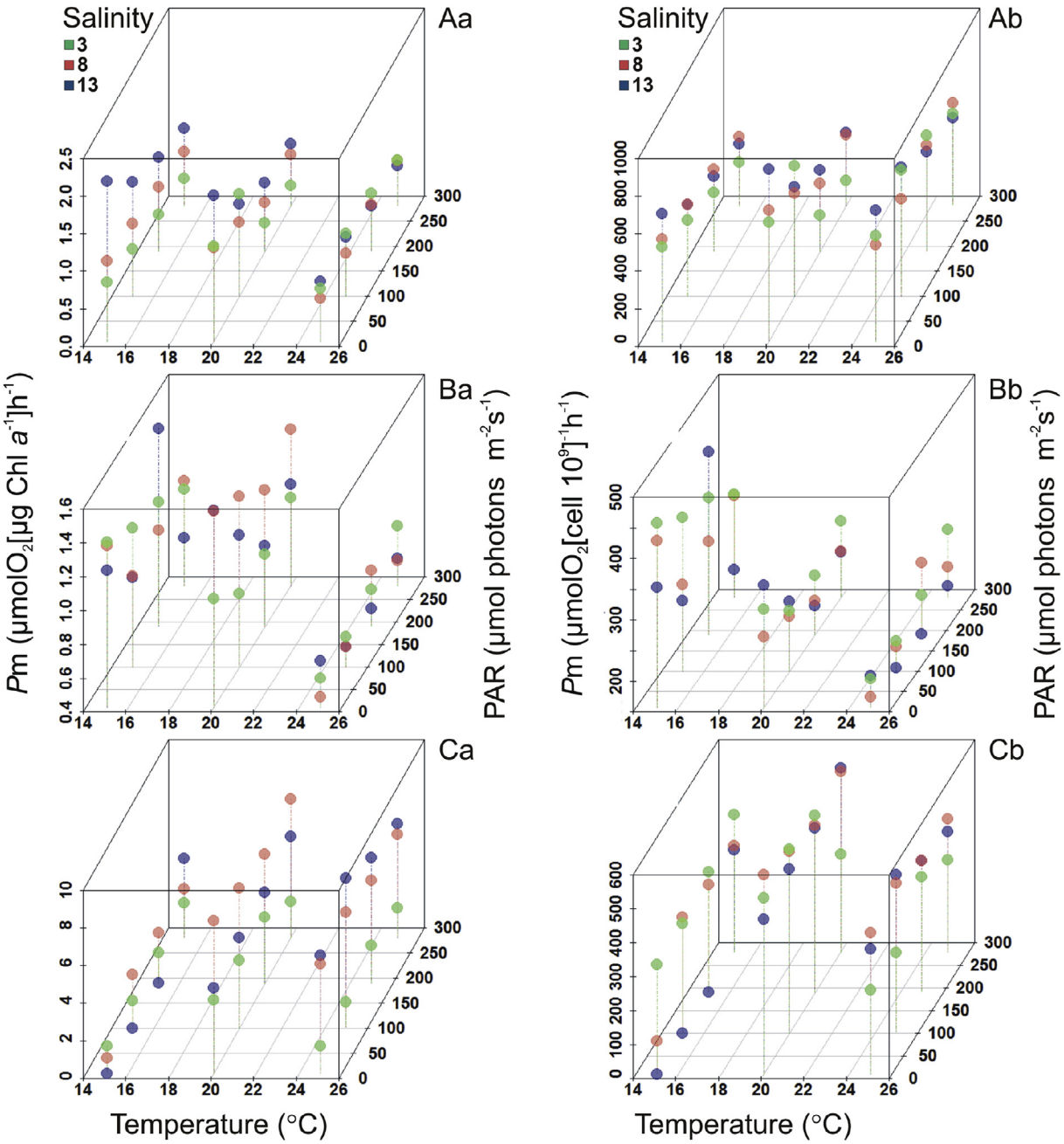

Fig. 4. The Chl *a*-specific (a) and cell-specific (b) photosynthesis capacity (Pm) for cyanobacterial strains: *N. spumigena* (A), *Aphanizomenon* sp. (B) and *D. lemmermannii* (C) after 7 d of cultivation at different PAR, temperature and salinity.

expressed per cell unit and remained constant at different growth conditions. In contrast, the Chl *a*-specific α in *N. spumigena* and *Aphanizomenon* sp. changed depending on environmental conditions. The maximum values in *N. spumigena* and *Aphanizomenon* sp. (0.016 and 0.017, respectively) were obtained at 10 µmol photons $m^{-2}s^{-1}$, 15 °C and salinity 8 (Fig. 5).

The net *P-E* curves (µmol O_2 [cell 10^9]$^{-1}h^{-1}$) and (µmol O_2 [µ Chl *a*]$^{-1}h^{-1}$) for the three species of cyanobacteria after one week of cultivation at different PAR (µmol photons $m^{-2}s^{-1}$), temperature (°C) and salinity were also analyzed (Fig. 6). Based on the *P-E* curves, two mechanisms of photoacclimation could be recognized in the cyanobacterial strains. The maximum value of P_m expressed per cell unit at the lowest light (10 µmol photons $m^{-2}s^{-1}$) indicated a change in the number of Photosynthetic Units (PSU) in *N. spumigena* and *Aphanizomenon* sp. On the other hand, the constant values of α and the maximum value of P_m expressed per Chl *a* unit at the highest light (280 µmol photons $m^{-2}s^{-1}$) indicated a change in the PSU size in *D. lemmermannii*.

4. Discussion

Cyanobacteria are known to exhibit some already acknowledged fixed responses to environmental conditions, and it is recognized that the life cycle of filamentous cyanobacteria is dependent on multiple factors. The major of these are the atmospheric and land-originated nutrient inputs, the salinity of ambient waters, irradiance, temperature and wind conditions (Whitton and Potts, 2012). Nevertheless, the specific responses vary between individual species. In this study, the different cyanobacterial species exhibited various sensitivity to irradiance, temperature and salinity, which is consistent with the literature

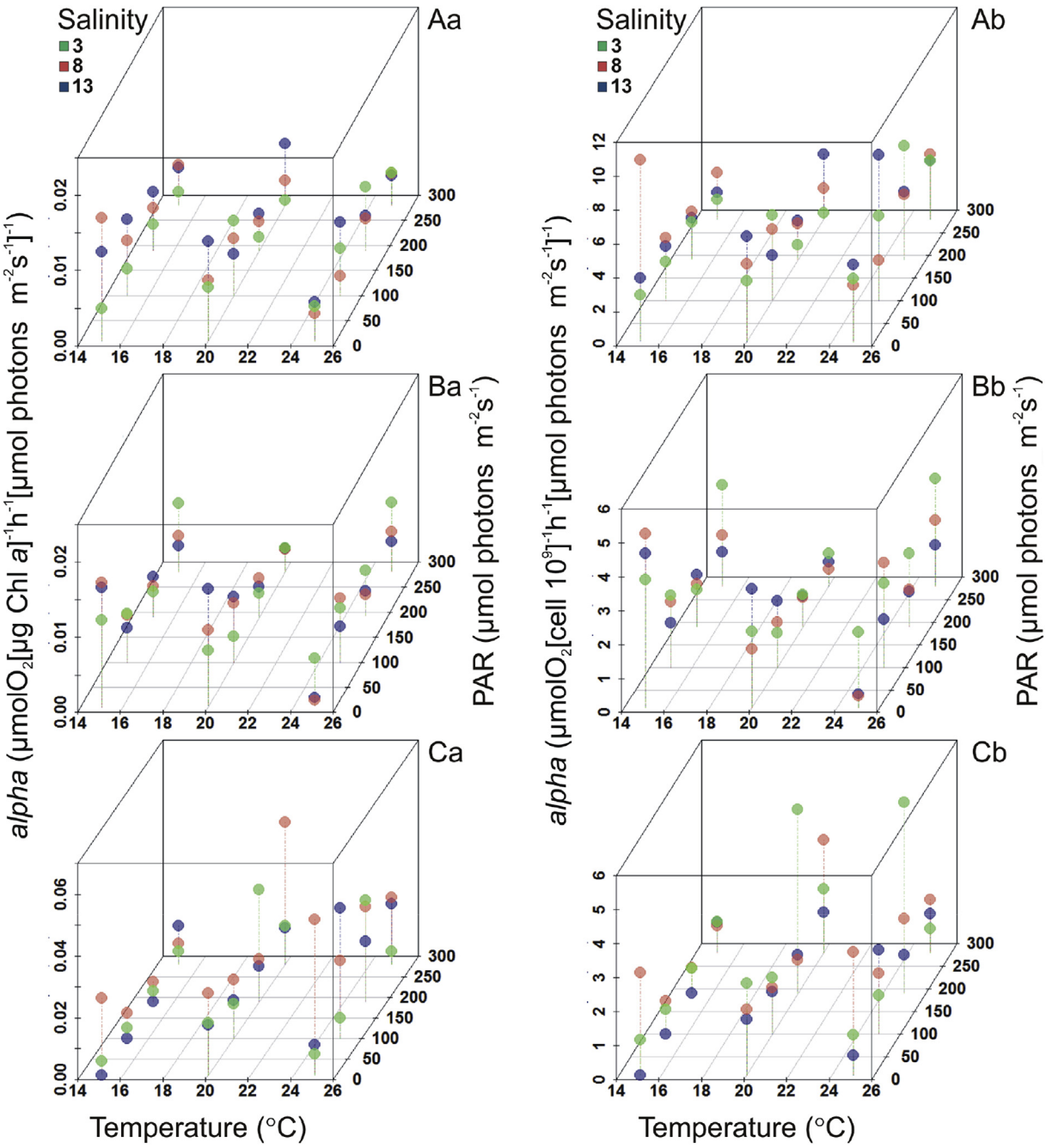

Fig. 5. The Chl *a*-specific (a) and cell-specific (b) photosynthetic efficiency at limiting irradiance (αlpha) for cyanobacterial strains: *N. spumigena* (A), *Aphanizomenon* sp. (B) and *D. lemmermannii* (C) after 7 d of cultivation at different PAR, temperature and salinity.

evidence (Jodłowska and Latała 2010, 2013; Jodłowska and Śliwińska, 2014; Brutemark et al., 2015).

Cyanobacteria are generally recognized to prefer low light intensity for growth (Fogg and Thake, 1987; Ibelings, 1996). Furthermore, as temperature increases, photosynthesis and respiration of cyanobacteria increase as well (Phinney and McIntire, 1965) until other factors, i.e., light and CO_2 limit the growth (Visser et al., 2006). However, each organism has a certain temperature- and light-related life spectrum, and even strains of the same species may have different requirements (Ignatiades and Smayda, 1970). Moreover, Jodłowska and Latała (2010) observed that *N. spumigena* was very highly tolerant of the highest irradiance applied (290 µmol photons $m^{-2}s^{-1}$) at low temperature (15 °C). The present research also indicated that the interaction of the two factors (temperature and PAR) played a key role in the growth process. However, the cell concentrations of *N. spumigena* under high PAR were similar at 15 and 20 °C, and lower than the respective densities in the highest temperature scenario (25 °C). Generally, the three species of filamentous cyanobacteria were found to be well acclimated to relatively high PAR levels. The acclimation was very pronounced at the high temperature treatment. This, in turn, is consistent with the observations reported by Jodłowska and Latała (2013) who tested the Baltic cyanobacterium *Geitlerinema amphibium* and found a promoting effect of increased irradiance and temperature on the cyanobacteria abundances. The maximum values of dry mass were recorded under the light intensities of 95–125 µmol photons $m^{-2}s^{-1}$ and at 22–30 °C, and they were almost 10 times the minimum values observed at about 15 °C within the whole range of light intensities tested. Moreover, based on their experiments with the filamentous

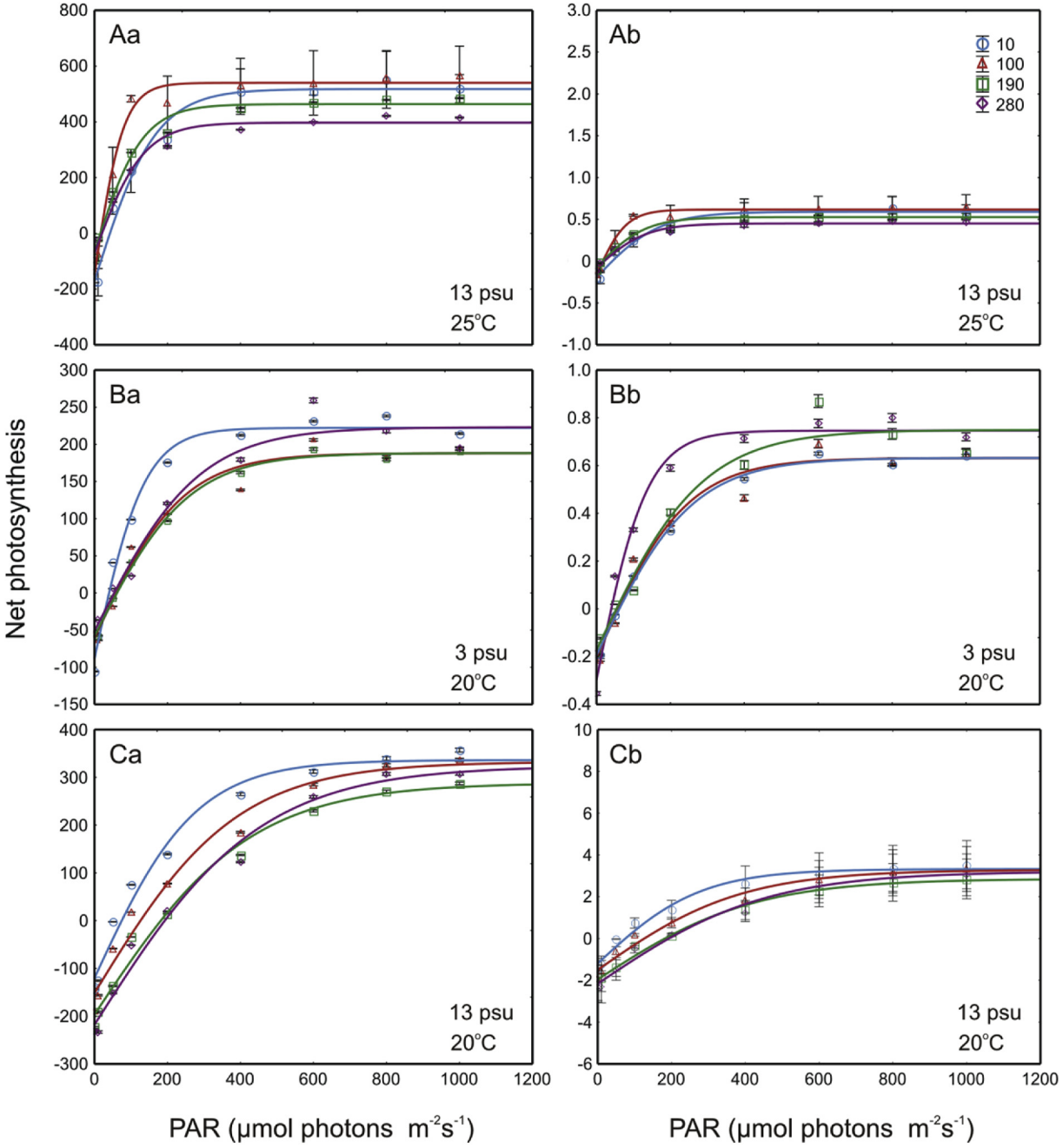

Fig. 6. Selected net photosynthetic rates: a, µmol O_2 [cell 10^9]$^{-1}$h^{-1} and b, µmol O_2 [µ Chl *a*]$^{-1}$h^{-1} for cyanobacterial strains: *N. spumigena* (A), *Aphanizomenon* sp. (B) and *D. lemmermannii* (C) after 7 d of cultivation at different PAR (µmol photons m^{-2}s^{-1}), temperature (°C) and salinity. The curves show examples of two types of photoacclimation observed in the cyanobacteria: a change in the number of Photosynthesis Units (PSU) (A, B) and a change in size of PSU (C).

cyanobacteria *Spirulina platensis*, Jensen and Knutsen (1993) noted that a temperature increase from 20 °C to 30 °C considerably reduced the photoinhibition as a result of D1 protein denaturation. As the studies mentioned above and the present research involved different filamentous cyanobacteria species, all these consistent findings may be assumed as representative for filamentous cyanobacteria in general.

Field studies on nitrogen-fixing species of cyanobacteria (*Aphanizomenon flos-aquae* and *N. spumigena*) in brackish waters showed that there may be a link between the temperature and the year-to-year differences in bloom intensities, e.g., a massive bloom of toxic *N. spumigena* occurred in July 1994 when the water temperature reached 22 °C (Pliński and Jóźwiak, 1999). The results presented here support the link. The bloom-forming cyanobacteria reached the highest abundances at the highest temperature tested. Moreover, the temperature of 10 °C was not a favorable condition to grow for all the species tested in this study (data not shown). The cells were unable to survive and develop under the low-temperature scenarios. The most substantial differences in abundances were observed with temperature changes. This may indicate that temperature was the most important factor for cyanobacteria growth, as stated by Davison (1991) and Roos and Vincent (1998). The positive response of cyanobacterial abundance and growth to the temperature increase is the essential conclusion in the context of climate change. Global warming promotes cyanobacteria blooms (O'Neil et al., 2012; Worden and Wilken, 2016; Paerl, 2018). In addition, a high sensitivity of filamentous cyanobacteria growth to a temperature change has been evident in regional numerical models developed for and applied to the Baltic Sea (Neumann et al., 2002). On the other hand, for the cyanobacteria bloom to occur, all the optimal

conditions have to occur simultaneously (Heisler et al., 2008); therefore, there are long-term predictions which either confirm or contest the opinion of bloom intensity increase to be an effect of global warming (Hense et al., 2013; Andersson et al., 2015b). Allowing for the impact of vertical mixing on cyanobacteria and following the present results with respect to temperature effects on the filamentous cyanobacteria abundances, the temperature may be regarded as the key hydrographic factor controlling the filamentous cyanobacteria bloom development in the Baltic Sea.

Field research has shown salinity from 3.8 to 11.5 to be an important factor for the spatial distribution of a cyanobacteria bloom in the Baltic Sea (Wasmund, 1997). During this study, the cyanobacteria cultures were also incubated at salinity 18 (data not shown) and the cultures failed to grow. The salinity seemed to be too high. The preference of the filamentous cyanobacteria studied to live in low- or moderate-salinity mediums has been already reported (Lehtimäki et al., 1997). However, it was striking that *N. spumigena* did not show any preference to survive at salinity 18. On the contrary, there are studies showing the ability of the Baltic *N. spumigena* to live within the salinity range from 5 to 20 (Lehtimäki et al., 1997) and to increase its abundance with salinity increase from freshwater in the north of the Baltic Sea to approximately 15 in the southern Baltic Proper (Niemistö et al., 1989). Note that salinity 20 is still much lower (by a factor of 0.57) than the average global ocean salinity (35). This study showed the filamentous cyanobacteria to not thrive at a high salinity; the abundances decreased as the salinity increased. Furthermore, Brutemark et al. (2015) demonstrated experimentally that the toxicity and allelopathic potential of the brackish *Dolichospermum* sp. varied significantly between salinities. Based on three salinity levels tested: 0, 3 and 6 they concluded that the highest allelopathic potential was observed at the intermediate salinity, the lowest potential being shown in the freshwater medium. In addition, the amount of the intracellular toxin (microcystin) was the highest at salinity 6. Moreover, analysis of monitoring data from the northern Baltic Proper and the Gulf of Finland showed an increase in the *Dolichospermum* sp. biomass between 1979 and 2013 in concert with a salinity decrease (Brutemark et al., 2015). This points to a strong influence of salinity on different aspects of cyanobacterial life cycles and distributions in water basins. On account of positive trends in precipitation and land-originated water inflow (Graham, 2004; Kjellström and Ruosteenoja, 2007), salinity in some of the Baltic Sea basins may decrease considerably within the next decades (Suikkanen et al. 2007, 2013). This might be an important driver for cyanobacteria bloom predictions and their ecological effects in the whole ecosystem.

Surface and near-surface populations experience extremely variable light, temperature and salinity conditions; these factors affect the photosynthesis performance and composition of the photosynthetic pigments of cyanobacteria (Jodłowska and Latała 2010, 2013; Jodłowska and Śliwińska, 2014). The results for *N. spumigena*, *Aphanizomenon* sp. and *D. lemmermannii* show two photoadaptive models (Richardson et al., 1983). The cyanobacteria acclimated to various environmental conditions exhibited a change in the number of Photosynthetic Units (PSU) (*N. spumigena* and *Aphanizomenon* sp.) and a change in PSU size (*D. lemmermannii*). The fluorescence measurements of all the cyanobacteria strains tested indicated that high irradiance and high temperature had a negative effect on ΦPSII. Furthermore, *N. spumigena*, *Aphanizomenon* sp. and *D. lemmermannii* were found to be able to adjust the suite of photosynthetic pigments their cells contained. The highest Car/Chl *a* ratios were observed at a high irradiance. The results obtained in the present study indicated also that in some scenarios, a high PAR had a negative effect on Chl *a* and Car cell concentrations, which was especially pronounced in the *D. lemmermannii* cultures. Additionally, the Car content decreased as the salinity increased. Since carotenoids play an important role in the cells as a protection against photooxidation (Siefermann-Harms, 1987; Majchrowski and Ostrowska, 1999), the present study confirms their role in enabling *N. spumigena*, *Aphanizomenon* sp. and *D. lemmermannii* to reach high abundances within a wide range of light and temperature conditions, but not in highly saline and very low-temperature water masses.

The results strongly emphasize the difference in filamentous cyanobacteria preferences to various environmental conditions and suggest that the distribution and contribution of the cyanobacteria strains to summer blooms may vary depending on the water properties. Moreover, the filamentous cyanobacteria contribution to the primary production may change as the effect of global warming and reduction in salinity. The studies referred to above (Graham, 2004; Kjellström and Ruosteenoja, 2007) concluded that the climate change would bring more preferable circumstances for cyanobacteria to grow. On the other hand, as has been demonstrated in this study, cyanobacteria are able to extend their life preferences and tolerate a wide range of environmental conditions.

Other aspects of the presence of cyanobacteria, e.g. the mechanisms of toxin release regulation, are still poorly understood. Nevertheless, Walls et al. (2018) found out that warming ≥ 20 °C would result in a 36% increase in toxin release by a freshwater cyanobacteria species. Moreover, research on allelopathic activity revealed that the smallest cyanobacteria (picocyanobacteria) may inhibit growth of the filamentous cyanobacteria (Śliwińska-Wilczewska et al., 2017; Barreiro Felpeto et al., 2018b). Studies on such interactions may lead to advance our knowledge concerning cyanobacteria life cycle details. They would result in more accurate long-term predictions of cyanobacterial abundances and bloom duration as well as in a more in-depth exploration of cyanobacterial effects on the whole ecosystem. Secondary metabolites and the allelopathy potential of different cyanobacterial size fractions is a recent research avenue which still needs further exploration.

5. Conclusions

The differences and similarities between the autecologies of three species of bloom-forming cyanobacteria were described. Generally, the filamentous cyanobacteria abundance was found to respond positively to PAR and temperature increase, and an adverse effect of salinity increase on the cyanobacteria abundance was noted. Effects on the pigment content, photosynthesis and Chl *a* fluorescence parameters were tested in 36 environmental scenarios. The study provided insights leading to further research on different aspects of competition between marine phytoplankton organisms: competition for nutrients, allelopathic potential, and toxin excretion. Moreover, the in-depth knowledge on filamentous cyanobacteria ecophysiology enables development of reliable predictions of their abundance in the future and long-term scenarios of the ecosystem response to the changing environment. The results presented in this paper may be extrapolated to all freshwater and brackish environments with a similar cyanobacteria community composition.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2019.01.016.

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